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REVIEW, CONCEPT, AND SYNTHESIS

A review on the biodiversity, distribution and trophic role of cephalopods in the Arctic and Antarctic marine ecosystems under a changing ocean

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Abstract

Cephalopods play an important role in polar marine ecosystems. In this review, we compare the biodiversity, distribution and trophic role of cephalopods in the Arctic and in the Antarctic. Thirty-two species have been reported from the Arctic, 62 if the Pacific Subarctic is included, with only two species distributed across both these Arctic areas. In comparison, 54 species are known from the Antarctic. These polar regions share 15 families and 13 genera of cephalopods, with the giant squid *Architeuthis dux* the only species confirmed to occur in both the Arctic and Antarctic. Polar cephalopods prey on crustaceans, fish, and other cephalopods (including cannibalism), whereas predators include fish, other cephalopods, seabirds, seals and whales. In terms of differences between the cephalopod predators in the polar regions, more Antarctic seabird species feed on cephalopods than Arctic seabirds species, whereas more Arctic mammal species feed on cephalopods than Antarctic mammal species. Cephalopods from these regions are likely to be more influenced by climate change than those from the rest of the World: Arctic fauna is more subjected to increasing temperatures per se, with these changes leading to increased species ranges and probably abundance. Antarctic species are likely to be influenced by changes in (1) mesoscale oceanography (2) the position of oceanic fronts (3) sea ice extent, and (4) ocean acidification. Polar cephalopods may have the capacity to adapt to changes in their environment, but more studies are required on taxonomy, distribution, ocean acidification and ecology.

Introduction

The polar regions play an important role in Earth's processes (Allison et al. 2009; Krupnik et al. 2011). As polar environments are changing faster than any other region on Earth, changes have implications regionally and globally (Sarmiento et al. 2004; IPCC 2013; Meltofte 2013; Kennicutt et al. 2014, 2015; Screen and Francis 2016). For example, ocean temperatures in the Antarctic have increased to 0.17 °C (from 1950 to 1980 period), while the Arctic Ocean temperature has increased to 1.3 °C (from 1990 to 2005 period) (Gille 2002; Walczowski and Piechura 2006), and more than 2 °C in some areas (since the 1960's) (IPCC 2001; Moritz et al. 2002; Vaughan et al. 2003). Furthermore, polar

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amplification in the Arctic (i.e., larger change in temperature near the poles in relation to the rest of the planet) is expected to be 1.5–4.5 times higher which can lead to future global warming (Holland and Bitz 2003), and it is much larger in Greenland than in central Antarctica (Masson-Delmotte et al. 2006). With such changes in the physical environments, various polar species will be affected by the climate change (Atkinson et al. 2004; Post et al. 2009; Convey et al. 2012; Constable et al. 2014). Regarding natural resources (besides fisheries), it is important to note that about 10% of the world's oil resources and 25% of gas resources are located in the Arctic (Thurston 2008), whereas the Antarctic holds 90% of Earth's ice and about 70% of its freshwater (Kennicutt et al. 2014). Moreover, the Arctic is home to more than four million people (Meltofte et al. 2013; IASC 2015; Kennicutt et al. 2015), whereas Antarctica has no indigenous populations.

The borders of the Arctic region are not firmly defined and have been treated differently by different authors (Nesis 1985, 1987b, 2003; Treshnikov 1985; Briggs 1995; AMAP 1998; AHDR 2004; Longhurst 2007; Spalding et al. 2007, 2012). In this review, we consider the Arctic to extend from the Pacific shelf part of the Bering Sea to the southern parts of the Denmark and Davis Straits on the Atlantic side, including the Faroe-Iceland Ridge and Faroe-Shetland Channel (Fig. 1). On the Atlantic side, two of the most commonly used Arctic maps (AMAP 1998; AHDR 2004) include the Faroe area but not the Shetlands, such that the border crosses the Faroe-Shetland Channel. Our scheme is different only in that it includes the full Faroe-Shetland Channel and is in line with modern nested biogeographical provinces (Longhurst 2007; Spalding et al. 2007, 2012; Watling et al. 2013) as well as with classical physiographic maps of the Arctic (Nesis 1985, 1987b; Treshnikov 1985; NOAA 1988) and has been used before (Nesis 1985, 1987b, 2003; Spalding et al. 2012). The border of the Arctic with the Pacific is based on oceanography: most warm-water masses do not reach the shelf areas of the Bering Sea (Loughlin and Kiyotaka 1999), which is consequently cold and shallow, similar to the eastern Arctic seas (Mironov 2013). Still, some authors either consider all of the Bering Sea as part of the Arctic (AMAP 1998; AHDR 2004; Spalding et al. 2007) or draw the border between the regions in the Bering Strait (Treshnikov 1985; Longhurst 2007; Mironov 2013). Therefore, in this study information in the literature on the cephalopod fauna of the slope and deep-water areas of the Bering Sea (referred to as Pacific Subarctic) were analysed separately to show that in relation to cephalopod biogeography this area is different. Our study considered the Antarctic region (i.e., Antarctic continent and its surrounding deep-water Ocean) to be south of the Antarctic Polar Front (APF), also known as the Antarctic convergence (Fig. 2). The Antarctic continental shelves are unusually deep (Orsi et al. 1995; Xavier et al. 1999; Walton 2013) in comparison with the Arctic (Ainley and DeMaster 1990) which affects the organisms living there.

Fig. 1 Arctic region. The borders shown are combined basing on various studies (Nesis 1985, 1987b, 2003; Treshnikov 1985; Briggs 1995; AMAP 1998; Loughlin and Kiyotaka 1999; AHDR 2004; Longhurst 2007; Spalding et al. 2007, 2012; Mironov 2013). Pacific Subarctic region (see "Introduction") lies to the south from the line in the Bering Sea

Polar marine organisms live permanently in low temperatures and may be subjected to environmental variability and to extreme events (Thomas et al. 2008; Meltofte et al. 2013; Xavier and Peck 2015). The range of marine habitats in both polar regions is as broad as that of the adjacent temperate climate zones; the Arctic region is characterized by extensive, shallow shelf seas surrounding a largely land-locked ocean, whereas the Antarctic region is dominated by a land-remote, dynamic, open ocean (Smetacek and Nicol 2005). There are contrasting general patterns of biodiversity in the Arctic and the Southern Ocean (Convey et al. 2012; Verde et al. 2012) and although marine food web structure may be similar in different regions, the individual species that dominate mid-trophic levels vary across polar regions (Dayton et al. 1994; Murphy et al. 2016). For example, krill (family Euphausiidae)

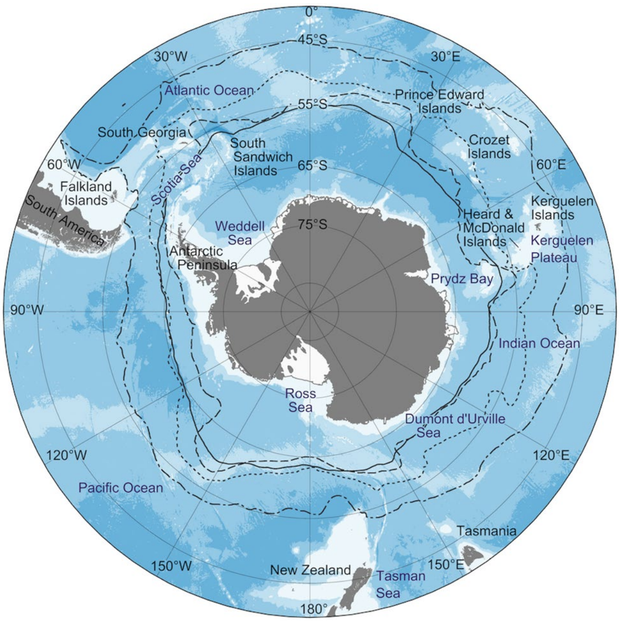

Fig. 2 Antarctic region. The solid line shows the mean maximum extent of sea ice (Raymond 2014), the dashed line shows the mean position of the Southern Antarctic Circumpolar Current Front (SACCF), the dotted line the Antarctic Polar Front (APF), and the dash–dotted line the Sub-Antarctic Front (SAF) (Sokolov and Rintoul 2009)

generally appear less abundant in Arctic Ocean waters than in Antarctic waters (McBride et al. 2014); Antarctic krill *Euphausia superba* plays an important role in Southern Ocean marine ecosystems (Everson 2000), whereas in the northern hemisphere, this role is occupied by several species of planktonic crustaceans (Calanoid copepods, euphausiids) and fish, with Arctic cod *Boreogadus saida* considered one of the most important species (Ainley and DeMaster 1990; Hop and Gjøsæter 2013; Murphy et al. 2016). The diversity of air-breathing predators (e.g., baleen whales, toothed whales, walruses *Odobenus rosmarus*, bears, seals, seabirds) present in the polar regions is driven by the biological composition of the food webs in the Arctic and Antarctic (Ainley and DeMaster 1990) (see above; e.g., high availability of Antarctic krill in the Antarctic able to supply a large number of predators) and is restricted to those able to survive in cold physical environments (the Southern Ocean is relatively more homogeneous seasonally and spatially than the Arctic Ocean). A direct comparison of species lists from polar regions during the Census of Marine Life suggested there could be as many as 230 metazoan bipolar species; however, recent studies have taken a more conservative view, concluding that, while bipolar species are probably natural transient phenomena, reported numbers might be inflated by a lack of in depth taxonomy (Gutt et al. 2010; Allcock and Griffiths 2014). There are no recent studies comparing the cephalopod fauna of both polar regions, other than a compilation of cephalopod species in major fishing areas of the world (Jereb and Roper 2005, 2010; Jereb et al. 2014). Nesis (1985) did provide a list of genera and some species in polar regions and concluded: (1) there are more cephalopod species/genera in the Antarctic than in the Arctic; (2) the Antarctic fauna of cephalopods has more endemics, and (3) the Antarctic fauna of cephalopods is more ancient.

Cephalopods are widely recognized as playing a pivotal role in many marine ecosystems, both as predators and prey (Clarke 1996; Boyle and Rodhouse 2005; Jereb and Roper 2010; Jereb et al. 2014; Xavier et al. 2015). Some cephalopods (i.e., oceanic squid) have a short lifespan (~ < 1–2 years), rapid growth and semelparous maturation patterns (Arkhipkin 2004; Boyle and Rodhouse 2005), while others (e.g., some octopods and nautiluses) may have longer lifespans (> 4 years) (Saunders 1984; Robison et al. 2014). These life cycle traits may have positive or negative effects on cephalopod species in relation to environmental change, as cephalopods can be both sensitive (in terms of rapid response) and resilient (in terms of recovery) to phenomena such as overfishing or climate variability and change (Pecl and Jackson 2008; Rosa and Seibel 2008; André et al. 2010; Pierce et al. 2010; Rodhouse 2013; Hoving et al. 2014; Rodhouse et al. 2014b).

The Arctic is warming due to the increased heat content of Atlantic water masses entering the Central Polar Basin mainly via the Spitsbergen current (Walther et al. 2002; Hassol 2005; Walczowski and Piechura 2006; Walsh 2008; Boitsov et al. 2012), which is causing the spread of Atlantic invertebrates and fish into this area (Berge et al. 2005; Johannesen et al. 2012; Nekhaev 2013). At the other polar region, manifold regional change (e.g., shifts in water temperature, ice sheet extent, currents and oceanic front positions, stratification, westerly winds) has been reported from the Antarctic landmass and its surrounding Southern Ocean over the last 30 years (Turner et al. 2009, 2014; Constable et al. 2014; Gutt et al. 2015). The impact of climate change on Arctic and Antarctic cephalopods has been partly addressed (Golikov et al. 2013b; Rodhouse 2013). However, exactly how this, and other phenomena affect polar cephalopods is not yet fully understood (Ainley and DeMaster 1990; Xavier et al. 2015). In this study, we aim to provide a broad comparative review of the biodiversity, distribution and trophic ecology of cephalopods from polar regions, under a climate change context.

Biodiversity

Arctic (including Pacific Subarctic)

The cephalopod fauna of the Arctic (including Pacific Subarctic) includes octopods, oegopsid squid and sepiolids, but other major groups of cephalopods (namely loliginid squid and sepiids) are absent (Fig. 1, Tables 1, 2). It is also noteworthy that no species are circumpolar which could be due to lack of adequate cephalopod sampling in the region. Indeed, *Rossia moelleri*, *Gonatus fabricii* and *Bathypolypus arcticus* could possibly have a circumpolar distribution (Young 1973; Nesis 1985, 1987b). Overall, there are 32 species from 15 families of cephalopods in the Arctic, expanding to 62 species (and 19 families) when the Pacific Subarctic is included. The incirrate octopods (nine for the Arctic and 16 species together with the Pacific Subarctic) and sepiolids (nine species for the Arctic and 10 species together with the Pacific Subarctic) inhabit the sea floor, while the cirrate octopods (three for the Arctic and five species together with the Pacific Subarctic) are mostly benthopelagic organisms (Fig. 1). A few squid species are neritic and demersal (two species for the Arctic from its Atlantic side), but most (nine for the Arctic and 29 species together with the Pacific Subarctic) inhabit meso- and bathypelagic layers (Table 1).

Only 10 species of cephalopods are found in high Arctic latitudes and complete their entire life cycle (including reproduction) in the Arctic. These are *Cirroteuthis muelleri* (cirrate), *Bathypolypus arcticus*, *B. bairdii*, *B. pugniger*, *Muusoctopus* sp., *M. sibiricus* and *M. leioderma* (incirrates), *Rossia palpebrosa* and *R. moelleri* (sepiolids), and *Gonatus fabricii* (pelagic squid) (Grieg 1933a; Grimpe 1933; Nesis 1985, 1987b, 2001; Bjørke and Gjøsæter 2004; Gardiner and Dick 2010a; Golikov et al. 2013a, b). All other species are occasionally distributed in the border areas of the Arctic, and/or appear in higher latitudes due to warming conditions and/or for foraging episodes (Mercer 1969; Nesis 1985, 1987b; Willassen 1986; Sabirov et al. 2009, 2012; Golikov et al. 2013b, 2014). Interestingly, only one species, *M. leioderma*, can be constantly found in both the Arctic and Pacific Subarctic regions. *Berryteuthis magister* occurs infrequently in the border regions of the Arctic, and it is an abundant commercial species in the Pacific Subarctic. All other cephalopod species inhabit one or the other of the two regions (Table 1). This is evidence from cephalopods that the Bering Sea slope and deep-water parts should not be considered as the Arctic, which is in line with modern biogeographical views on nested provinces (Spalding et al. 2007, 2012; Mironov 2013; Watling et al. 2013).

The data in Table 1, compiled from published sources and unpublished data, list every cephalopod species found in the Arctic and Pacific Subarctic with notes on the distribution of that species in the area. There are nine species, previously recorded from the area which, according to us, are erroneous records:

Octopods:

1. *Cirrothauma murrayi* was recorded in the centre of the Arctic Ocean (Voss 1967; Mohr and Geiger 1968; Aldred et al. 1983). According to Nesis (1987a), it is doubtful that the deepest-living (abyssopelagic) species of cirrate entered the Arctic through passages in the ridges separating the Arctic from the North Atlantic (the northernmost point of distribution in the Atlantic is its subtropical part) and then exhibited positive phototaxis (the doubtful specimen was caught at the surface through a hole in the ice). The location of the specimen has been unknown since 1967, and its identification has not, therefore, been checked, with subsequent mentions in the literature all citing just one paper (Voss 1967).
2. *Muusoctopus hokkaidensis* and
3. *M. profundorum* were recorded at the shelf part of the Bering Sea and border areas with the Chukchi Sea (Kondakov 1948; MacGinitie 1955; Akimushkin 1965). In later papers (Kondakov et al. 1981; Nesis 1987a), some specimens were treated as *M. sibiricus* and *Muusoctopus* sp. The latter species is also considered to be *M. sibiricus* (I. Gleadall pers. comm.). So, *M. hokkaidensis* and *M. profundorum*, like other North Pacific octopods shown in Table 1, inhabit only the Pacific Subarctic.

Oegopsids:

4. Records of *Onychoteuthis banksi* on the Norwegian shelf at about 70°N (Sars 1878) are believed to be misidentifications of the common arctic squid *Gonatus fabricii* (Nesis 1987b).
5. Records of *Onykia robusta* in the shelf part of the Bering Sea (Kondakov 1948; Mercer 1969) were considered to be incorrect soon after publication (Akimushkin 1965; Nesis 1987a, b). This species inhabits only the Pacific Subarctic (Jereb and Roper 2010). The records from the shelf part were based on beaks in sperm whales (Kondakov 1948; Akimushkin 1965; Mercer 1969), which obviously consumed them within the species range.
6. Remains of *Ommastrephes bartrami* are recorded in deep-water fish in the Spitsbergen area and to the north of Davis Strait (Steenstrup 1880). All other papers mentioning *O. bartrami* from the area (Bruun 1945; Nesis 1987b) cite Steenstrup's record. It is suggested that this species was eaten within its usual range, meaning far outside the Arctic (Nesis 1987b).

All the above-mentioned squid are obviously warm-water species and certainly do not inhabit such northern areas (Nesis 1987a, 1987b; Jereb and Roper 2010).

Sepiolids (bobtail squid):

7. Records of *Semirossia tenera* in the Spitsbergen area (Grimpe 1933) and in the Kara Sea (Kondakov 1948) are obviously erroneous. This is a western Atlantic subtropical species (Nesis 1987b; Jereb and Roper 2005). It was not even found in the western Atlantic Subarctic by Mercer (1968), while studying bobtail squid species living in the area: only species of the genus *Rossia* were found.

Table 1 Arctic (including Pacific Subarctic) distribution of cephalopods

Species	Bathymetry	Geographic range (inside the studied area)	References
Opisthoteuthis borealis (Opisthoteuthidae)[a]	Mb	East and west coasts of Greenland	Collins (2002, 2005)
Opisthoteuthis albatrossi (Opisthoteuthidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Sasaki (1929), Kondakov (1941), Akimushkin (1965), Jereb et al. (2014)
Opisthoteuthis californiana (Opisthoteuthidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Sasaki (1929), Kondakov (1941), Akimushkin (1965), Jorgensen (2009), Jereb et al. (2014)
Cirroteuthis muelleri (Cirroteuthidae)[a]	Mb	Central Polar Basin, deep-water areas of the Norwegian, Greenland, Baffin seas and adjacent north Atlantic waters	Grieg (1933a), Nesis (1987a, b), Allcock et al. (2003b), Bjørke and Gjøsæter (2004), Jereb et al. (2014)
Stauroteuthis syrtensis (Stauroteuthidae)[a]	Mb	Deep-water north Atlantic up to east and west coasts of Greenland	Nesis (1987a), Frandsen and Zumholz (2004)
Eledone cirrhosa (Eledonidae)[a]	Sh	Norwegian shelf up to 70°N, Iceland	Nordgaard (1923), Nielsen (1930), Grieg (1933b), Grimpe (1933), Adam (1939), Bruun (1945), Muus (1959), Jereb et al. (2015)
Graneledone verrucosa (Megaleledonidae)[a]	Sl	North Atlantic up to 65°N	Bruun (1945), Mercer (1969), Allcock et al. (2003a), Jereb et al. (2014)
Graneledone boreopacifica (Megaleledonidae)[b]	Sl	Slope and deep-sea part of the Bering Sea	Jorgensen (2009), Jereb et al. (2014)
Bathypolypus arcticus (Bathypolypodidae)[a]	Sh, Sl	Almost circumpolar at the Arctic shelf and slope, down to southern Greenland and areas to the south of Davis Strait	Nesis (1987b), Muus (2002), Jereb et al. (2014)
Bathypolypus bairdii (Bathypolypodidae)[a]	Sh, Sl	North Atlantic up to Disko Bay (western Greenland), Iceland and south-western part of the Barents Sea	Muus (2002), Gardiner and Dick (2010b), Jereb et al. (2014)
Bathypolypus pugniger (Bathypolypodidae)[a]	Sh, Sl	The Davis Strait, Iceland, Faroes; seems to inhabit "border" areas of ranges of *B. arcticus* and *B. bairdii*	Muus (2002), Frandsen and Zumholz (2004), Gardiner and Dick (2010b), Jereb et al. (2014)
Muusoctopus sibiricus (Enteroctopodidae)[a]	Sh	Laptev, East-Siberian, Chukchi and Beaufort Seas	Løyning (1930), Kondakov et al. (1981), Nesis (2001)
Muusoctopus sp. (Enteroctopodidae)[d,a]	Sl	Around the Spitsbergen Archipelago from deep-water sides, slope of the northern Barents and Kara Seas, St. Anna's Trough	Nesis (2001), Allcock et al. (2006), Golikov et al. (unpubl. data)
Muusoctopus leioderma (Enteroctopodidae)[c]	Sh, Sl	The Bering Sea, southern part of the Chukchi Sea	Nesis (1987a, b), Jorgensen (2009), Jereb et al. (2014)
Muusoctopus hokkaidensis (Enteroctopodidae)[b]	Sh, Sl	Slope and deep-sea part of the Bering Sea	Nesis (1987a, b), Jorgensen (2009), Jereb et al. (2014)
Muusoctopus profundorum (Enteroctopodidae)[b]	Sh, Sl	Slope and deep-sea part of the Bering Sea	Jorgensen (2009), Jereb et al. (2014)
Muusoctopus oregonensis (Enteroctopodidae)[b]	Sh, Sl	Slope and deep-sea part of the Bering Sea	Nesis (1987a), Jorgensen (2009), Jereb et al. (2014)
Sasakiopus salebrosus (Enteroctopodidae)[b]	Sh, Sl	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Nesis (1987a), Jorgensen (2009), Jorgensen et al. (2010)
Enteroctopus dofleini (Enteroctopodidae)[b]	Sh, Sl	Slope and deep-sea part of the Bering Sea	Hartwick (1983), Jorgensen (2009)
Japetella diaphana (Amphitretidae)[b]	M	Slope and deep-sea part of the Bering Sea	Jorgensen (2009), Jereb et al. (2014)
Haliphron atlanticus (Alloposidae)[a]	Mb	North Atlantic, but there are two records from the Norwegian coast at 66.3°N–68.3°N	Willassen (1986), Bjørke and Gjøsæter (2004)
Onychoteuthis borealijaponica (Onychoteuthidae)[b]	Em	Slope and deep-sea part of the Bering Sea	Nesis (1987a), Kubodera et al. (1998), Jereb and Roper (2010)
Onykia robusta (Onychoteuthidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Nesis (1987a), Kubodera et al. (1998), Jereb and Roper (2010)

Table 1 (continued)

Species	Bathymetry	Geographic range (inside the studied area)	References
Gonatus fabricii (Gonatidae)[a]	Mb	Central Polar basin, the Norwegian, Greenland, Baffin Seas and adjacent north Atlantic waters, the Barents Sea and St. Anna's Trough in the Kara Sea	Grieg (1933a, b), Young (1973), Kristensen (1983), Nesis (1987a, b), Bjørke and Gjøsæter (2004), Jereb and Roper (2010), Golikov et al. (2012, 2013b)
Gonatus steenstrupi (Gonatidae)[a]	M	North Atlantic up to 63°N	Kristensen (1981), Nesis (1987a, b), Jereb and Roper (2010)
Gonatus berryi (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Kubodera and Jefferts (1984a, b), Nesis (1997), Jereb and Roper (2010)
Gonatus kamtschaticus (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Kubodera and Jefferts (1984a, b), Nesis (1997), Jorgensen (2007, 2009), Jereb and Roper (2010)
Gonatus madokai (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Kubodera and Jefferts (1984a, b), Nesis (1997), Jorgensen (2007, 2009), Jereb and Roper (2010)
Gonatus onyx (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Kubodera and Jefferts (1984a, b), Nesis (1997), Jorgensen (2007, 2009), Jereb and Roper (2010)
Gonatus pyros (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Okutani et al. (1988), Nesis (1997), Jereb and Roper (2010)
Gonatus ursabrunae (Gonatidae)[b]	M	Slope and deep-sea part of the Bering Sea	Kubodera and Jefferts (1984a, b), Okutani et al. (1988), Jereb and Roper (2010)
Gonatopsis borealis (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Kubodera and Jefferts 1984a, b), Okutani et al. (1988), Nesis (1997), Jorgensen (2007, 2009); Jereb and Roper (2010)
Gonatopsis japonicus (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Okutani et al. (1988), Nesis (1997), Jereb and Roper (2010)
Gonatopsis makko (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Okutani et al. (1988), Nesis (1997), Jereb and Roper (2010)
Gonatopsis octopedatus (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Kubodera and Jefferts (1984b), Okutani et al. (1988), Nesis (1997), Jereb and Roper (2010)
Gonatopsis okutanii (Gonatidae)[a]	Mb	Slope and deep-sea part of the Bering Sea	Jereb and Roper (2010)
Eogonatus tinro (Gonatidae)[a]	Mb	Slope and deep-sea part of the Bering Sea	Okutani et al. (1988), Nesis (1997), Jereb and Roper (2010)
Berryteuthis magister (Gonatidae)[c]	M	Slope and deep-sea part of the Bering Sea; few rare records from the shelf part of the Bering Sea	Akimushkin (1965), Nesis (1987b, 1997), Okutani et al. (1988), Jorgensen (2007, 2009), Jereb and Roper (2010)
Berryteuthis anonychus (Gonatidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Nesis (1997), Jorgensen (2007, 2009), Jereb and Roper (2010)
Histioteuthis bonnellii (Histioteuthidae)[a]	Mb	North Atlantic, but there is a record from the Davis Strait (63.5°N)	Kristensen (1980)
Stygmatoteuthis dofleini (Histioteuthidae)[b]	M	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Nesis (1994), Voss et al. (1998), Jereb and Roper (2010), Young and Vecchione (2015)
Brachioteuthis riisei (Brachioteuthidae)[a]	M	North Atlantic up to Davis Strait in the western part and to the Iceland and the south Norgenian Sea (63.5°N) in the eastern part	Nielsen (1930), Grieg (1933b), Grimpe (1933), Mercer (1969), Nesis (1987b), Frandsen and Zumholz (2004)
Architeuthis dux (Architeuthidae)[a]	Mb	Normally doesn't live to the north from the Northern Sea; single stranding specimens rarely reach norwegian shelf up to 70°N)	Nordgaard (1923), Grieg (1933b), Grimpe (1933), Bruun (1945), Muus (1959), Clarke (1966), Nesis (1987b), Bjørke and Gjøsæter (2004)
Illex illecebrosus (Ommastrephidae)[a]	Sh, Sl	Normally doesn't live in the Arctic; some years foraging shoals reach southern Greenland, Baffin Island and Iceland (up to 66°N)	Grimpe (1933), Bruun (1945), Mercer (1969), Nesis (1987a)

Table 1 (continued)

Species	Bathymetry	Geographic range (inside the studied area)	References
Todarodes sagittatus (Ommastrephidae)[a]	Sh, Sl	Normally does not live to the north from the Northern Sea; some years foraging shoals reach the Barents Sea, White and Kara Seas	Derjugin (1915), Nordgaard (1923), Nielsen (1930), Grieg (1933b), Grimpe (1933), Kondakov (1937), Adam (1939), Bruun (1945), Clarke (1966), Wiborg (1984), Nesis (1987b), Bjørke and Gjøsæter (2004), Golikov et al. (2013b)
Todaropsis eblanae (Ommastrephidae)[a]	M	Normally does not live to the north from the Northern Sea; due to the Arctic warming, reach the Southerrn Barents Sea	Sabirov et al. (2009, 2012)
Ommastrephes bartramii (Ommastrephidae)[b]	E	Normally does not live in the Arctic (see comments in text according to reports of these findings); single stranding specimens rarely reach slope and deep-sea part of the Bering Sea	Akimushkin (1965), Sinclair (1991), Jereb and Roper (2010)
Chiroteuthis calyx (Chiroteuthidae)[b]	M	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Nesis (1987a), Jorgensen (2009), Jereb and Roper (2010)
Mastigoteuthis agassizii (Mastigoteuthidae)[a]	Mb	Normally does not live in the Arctic; two specimens found in the Denmark Strait in 2002 (about 65.0°N)	Golikov et al. (in prep.)
Teuthowenia megalops (Cranchiidae)[a]	Mb	Up to 70°N in the Baffin Sea, to 66°N in the Denmark Strait and to 63°N in the Norwegian Sea; recently found in the eastern Greenland Sea about 74°N	Nesis (1965), Bjørke and Gjøsæter (2004), Frandsen and Zumholz (2004), Zumholz and Frandsen (2006), Golikov et al. (2013b)
Galiteuthis armata (Cranchiidae)[a]	Mb	Normally does not live in the Arctic; single specimen found in the Denmark Strait (about 65.6°N), probably due to Arctic warming	Golikov et al. (in prep.)
Galiteuthis phyllura (Cranchiidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Jereb and Roper (2010)
Taonius borealis (Cranchiidae)[b]	Mb	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Jereb and Roper (2010)
Rossia moelleri (Sepiolidae)[a]	Sh	Almost circumpolar at the high Arctic shelf, rare lower than 75°N; as exceptions occur at Jan-Mayen and down to 63°N in the Baffin Sea	Kondakov (1937), Mercer (1968, 1969), Nesis (1987b), Frandsen and Zumholz (2004), Zumholz and Frandsen (2006)
Rossia palpebrosa (Sepiolidae)[a]	Sh, Sl	Almost circumpolar at the Arctic shelf and slope, down to southern Greenland and areas to the south of Davis Strait in the western Atlantic and to the North Sea in the eastern Atlantic	Nordgaard (1923), Nielsen (1930), Grieg (1933a, b), Grimpe (1933), Kondakov (1937), Adam (1939), Bruun (1945), Akimushkin (1965), Mercer (1968, 1969), Nesis (1987b), Bjørke and Gjøsæter (2004), Frandsen and Zumholz (2004), Golikov et al. (2013a)
Rossia macrosoma (Sepiolidae)[a]	Sh, Sl	Northern part of the North Sea, norwegian shelf up to 68°N, Iceland, eastern Greenland (Franz-Joseph Fjord)	Nordgaard (1923), Grieg (1933b), Grimpe (1933), Adam (1939), Bruun (1945), Muus (1959, 1962), Jonsson and Dagsson (1970), Nesis (1987b)
Rossia megaptera (Sepiolidae)[a]	Sh, Sl	Western north Atlantic up to 70°N in the Baffin Sea. Research on distribution in the eastern Atlantic in progress	Verrill (1881), Mercer (1968, 1969), Nesis (1987b), Frandsen and Zumholz (2004), Golikov et al. (in prep.)
Rossia pacifica (Sepiolidae)[b]	Sh, Sl	Slope and deep-sea part of the Bering Sea	Akimushkin (1965), Mercer (1968, 1969), Jereb and Roper (2005)
Neorossia caroli (Sepiolidae)[a]	Sh, Sl	Northern part of the North Sea, Iceland	Adam (1939), Bruun (1945), Nesis et al. (2001)
Sepietta oweniana (Sepiolidae)[a]	Sh, Sl	Northern part of the North Sea, norwegian shelf up to 70°N; due to the Arctic warming reach the Tromsø Bank in the southern Barents Sea	Nielsen (1930), Grieg (1933b), Grimpe (1933), Bruun (1945), Bergstrøm and Summers (1983), Nesis (1987b), Golikov et al. (2014)

Table 1 (continued)

Species	Bathymetry	Geographic range (inside the studied area)	References
Sepiola atlantica (Sepiolidae)[a]	Sh	Northern part of the North Sea, norwegian shelf up to 63°N, Iceland	Grimpe (1925, 1933), Nielsen (1930), Grieg (1933b), Adam (1939), Bruun (1945), Yau and Boyle (1996)
Sepiola pfefferi (Sepiolidae)[a]	Sh	Northern part of the North Sea, norwegian shelf up to 63°N	Grimpe (1921, 1925, 1933), Bruun (1945)

E epipelagic, *Em* epi-mesopelagic, *M* mesopelagic, *Mb* meso-bathypelagic, *Sh* shelf, *Sl* slope

[a]Cephalopod species distributed in the Arctic, constantly or occasionally

[b]Cephalopod species distributed in Pacific Subarctic

[c]Cephalopod species distributed in Pacific Subarctic, which inhabit or occasionally spread into the Arctic

[d]*Muusoctopus* species from mentioned areas could be new species, or *M. normani* or *M. johnsonianus*; *M.* sp. from the Chukchi Sea MacGinitie (1955, 1959), Kondakov et al. (1981), Nesis (1987b) are identified as *M. sibiricus* by I. Gleadall. Also, in some papers *M. normani* is synonymized with *M. januarii* Gleadall (2013)

8. There is an erroneous record of *Sepiola rondeletii* in Greenland waters and around Ellesmere's Island (Mercer 1969; Gardiner and Dick 2010a). This bobtail squid is now believed to be a warmer-water species and the North Sea is the northernmost point of its distribution (Nesis 1987b; Jereb and Roper 2005). Actually, no Sepiolinae has ever been recorded in Greenland or further north (Mercer 1968).

   Ram's horn squid:

9. *Spirula spirula* is a tropical and subtropical ocean species, and its shells have been found on the shores of Canada at 69.75°N (Mercer 1969). This is the same phenomenon as when cuttlebones are washed ashore far from the known range of sepiids (Nesis 1987b): their gas-filled shells float and drift on oceanic currents after the animal has died.

Antarctic

The Antarctic cephalopod fauna is composed only of octopods, oceanic oegopsid squids and a sepiolid (Figs. 2, 3, Tables 3, 4). Loliginid squids, sepiids, vampire squid, and many octopod genera, including pelagic groups such as *Bolitaena*, *Japetella*, *Amphitretus* and *Eledonella*, are absent in the region (Allcock 2014; Rodhouse et al. 2014a; Xavier et al. 2016a) (Table 3).

Within octopods, 33 species from six families are known (Table 3), with the family Megaleledonidae (and its genus *Pareledone*) the most diverse, with new species still being discovered and described (Allcock 2005, 2014; Allcock et al. 2007). The incirrate octopod species of the genera *Pareledone* (13 species), *Megaleledone* (1 species) and *Adelieledone* (3 species) are endemic to the Antarctic (Allcock 2014).

In relation to Antarctic squids, 20 species from 13 families of squids are found in Antarctic waters (Table 3), with most (if not all) species having a circumpolar distribution (Rodhouse et al. 2014a; Xavier et al. 2016b). Of the known squid species, one is found only in Antarctic waters [south of the Antarctic Polar Front (APF)]: *Psychroteuthis glacialis.*

In summary, in terms of cephalopod biodiversity, 19 families occur in the Arctic (including Pacific Subarctic) and 20 in the Antarctic region (Fig. 3), with 15 of those occurring in both regions. No cuttlefish species occur today in the polar regions (Young et al. 1998; Xavier et al. 2016a). In fact, the lack of cuttlefish species in the Americas probably reflects the fact that there has been no warm-water colonization route, since the cold seas of the Oligocene led to the extinction of cuttlefishes from these areas (Khromov 1998). In terms of genera, the Arctic (including Pacific Subarctic) is home to 33 genera and the Antarctic 32 genera (Fig. 3), with 13 genera common to both regions. At the species level, while the Arctic has 62 species (including Pacific Subarctic;

Table 2 Prey and predators of Arctic and Pacific Subartic cephalopods

Species	Main prey	Main predators	References
Opisthoteuthis borealis	n/a	Greenland shark	Yano et al. (2007)
Opisthoteuthis californiana	Crustaceans: isopods, amphipods, mysids, crangonid/hippolytid shrimps	n/a	Pereyra (1965)
Stauroteuthis syrtensis	Crustaceans: mostly copepods	n/a	Vecchione and Young (1997)
Eledone cirrhosa	Mainly decapods: alpheid shrimps and brachyurans; other crustaceans; fish; cephalopods; gastropods; bivalves; polychaetes; echinoderms	Odontocetes; pinnipeds; sharks; osteichthyes; *Loligo forbesii*and *Architeuthis dux*	Jereb et al. (2015)
Graneledone boreopacifica	Gastropods and polychaetes	n/a	Voight (2000)
Bathypolypus arcticus[a]	Bristle stars; benthic crustaceans; mollusks; polychaetes	Sperm whale, narwhal; bearded seal, walrus; greenland shark; cod, greenland halibut	Finley and Gibb (1982), Finley and Evans (1983), Mehl (1991), Wood et al. (1998), Simon et al. (2003), Yano et al. (2007), Gardiner and Dick (2010a)
Bathypolypus bairdii[a]	Bristle stars; benthic crustaceans; mollusks; polychaetes	Sperm whale, narwhal; bearded seal, walrus; greenland shark; cod, greenland halibut	Finley and Gibb (1982), Finley and Evans (1983), Mehl (1991), Wood et al. (1998), Simon et al. (2003), Yano et al. (2007), Gardiner and Dick (2010a)
Muusoctopus sibiricus	n/a	Walrus	Løyning (1930)
Enteroctopus dofleini	Decapod crustaceans; bivalves, gastropods	Pinnipeds; fish	Hartwick (1983), Rigby and Sakurai (2004, 2005)
Japetella diaphana	n/a	Cuvier's beaked whale; blue shark; pelagic osteichthyes; *Ommastrephes bartramii*	Santos et al. (2001), Watanabe et al. (2004), Kubodera et al. (2007), Choy et al. (2013)
Haliphron atlanticus	Tunicates; shrimps *Pandalus borealis*; cnidarians: Scyphozoa and Cubozoa jellyfish	Sperm whale	Akimushkin (1965), Clarke and MacLeod (1976, 1982), Willassen (1986), O'Shea (2004), Hoving and Haddock (2017), Rosa et al. (2017)
Onychoteuthis borealijaponica	Small fish; cannibalism	Sperm whale, dolphins; fur seals; salmo shark; large pelagic osteichthyes; *Ommastrephes bartramii*	Okutani and Murata (1983), Watanabe et al. (2004), Kubodera et al. (2007), Jereb and Roper (2010)
Onykia robusta	Benthic fish; heart urchins; cnidarians	Sperm whale; pinnipeds	Akimushkin (1965), Nesis (1987a), Jereb and Roper (2010)
Gonatus fabricii	Before hooks appear: plankton crustaceans, pteropods and chaetognathes; after hooks appear: fish and cannibalism	Sperm whale, northern bottlenose whale, long-finned pilot whale, beluga whale, Sowerby's whale, beaked whale; hooded seal, harp seal, ringed seal, ribbon seal, spotted seal; puffins, fulmars, guillemots; greeland shark; cod, saithe, sea perch, grenadiers, blue ling, greenland halibut, coalfish, salmon and other fish; *Todarodes sagittatus*	Nesis (1965, 1971, 1987a, b), Kristensen (1977, 1983), Sennikov et al. (1989), Mehl (1991), Bjørke (1995, 2001), Barrett et al. (1997), Bjørke and Gjøsæter (1998), Arkhipkin and Bjørke (1999), Simon et al. (2003), Laidre et al. (2004), Gardiner and Dick (2010a)
Gonatus steenstrupi	n/a	Northern bottlenose whale, sperm whale and other odontocetes	Blanco et al. (1995), Bjørke (2001), Clarke (2006)
Gonatus berryi	Macroplankton crustaceans	Odontocetes; pinnipeds; fish; *Ommastrephes bartramii*	Nesis (1997), Jereb and Roper (2010)
Gonatus kamtschaticus	Macroplankton crustaceans; fish; squid	Odontocetes; pinnipeds; fish	Nesis (1997), Jereb and Roper (2010)

Table 2 (continued)

Species	Main prey	Main predators	References
Gonatus madokai	Macroplankton crustaceans; fish, squid	Odontocetes; pinnipeds; fish	Nesis (1997), Jereb and Roper (2010)
Gonatus onyx	Macroplankton crustaceans	Cuvier's beaked whale, Dall's porpoise; fish	Nesis (1997), Jereb and Roper (2010)
Gonatus pyros	n/a	Odontocetes; pinnipeds; fish	Nesis (1997), Jereb and Roper (2010)
Gonatopsis borealis	Macroplankton crustaceans; fish, squid; cnidarians	Odontocetes; pinnipeds; seabirds; fish; *Berryteuthis magister*; *Ommastrephes bartramii*; cannabilism	Nesis (1997), Jereb and Roper (2010)
Gonatopsis japonicus	Macroplankton crustaceans; fish	n/a	Nesis (1997), Jereb and Roper (2010)
Gonatopsis makko	n/a	Sperm whale	Nesis (1997), Jereb and Roper (2010)
Gonatopsis octopedatus	Macroplankton	Sperm whale; alaska pollock	Nesis (1997), Jereb and Roper (2010)
Eogonatus tinro	Macroplankton crustaceans	Northern fur seal; alaska pollock	Nesis (1997), Jereb and Roper (2010)
Berryteuthis magister	Macroplankton crustaceans: mainly euphausiids and hyperiid amphipods; small fish; other squid species, incl. cannibalism	Odontocetes; pinnipeds; seabirds; fish	Nesis (1997), Jereb and Roper (2010)
Berryteuthis anonychus	Macroplankton crustaceans; peropods; chaetognathes; cnidarians	Odontocetes; pinnipeds; seabirds; fish; *Ommastrephes bartramii*	Nesis (1997), Jereb and Roper (2010)
Histioteuthis bonnellii	n/a	Sperm whale, other odontocetes; blue shark; swordfish, tuna, lancetfish	Santos et al. (1995), Voss et al. (1998), Jereb and Roper (2010)
Stygmatoteuthis dofleini	n/a	Sperm whale, short-finned pilot whale, Hubb's beaked whale, other odontocetes; northern elephant seal; blue shark; swordfish	Akimushkin (1965), Nesis (1994), Voss et al. (1998), Kubodera et al. (2007), Jereb and Roper (2010)
Brachioteuthis riisei	Euphausiids	Sperm whale, stripped dolphin, short-beaked common dolphin; swordfish; giant red shrimp	Blanco et al. (1995), Clarke (2006), Jereb and Roper (2010)
Architeuthis dux	Macrourids, blue whitening, deep-sea pearch and other osteichthyes; other squid species, incl. cannibalism	Sperm whale; greenland shark; large pelagic osteichthyes	Clarke (1966, 2006), Förch (1998), Lordan et al. (1998), Bolstad and O'Shea (2004), Regueira et al. (2014)
Illex illecebrosus	Fish; pelagic crustaceans; pteropods; other squid species, incl. cannibalism	Odontocetes; pinnipeds; seabirds, elamobranchs; osteichthyes	Jereb and Roper (2010)
Todarodes sagittatus	Fish; pelagic crustaceans; pteropods; other squid species, incl. cannibalism	Odontocetes; pinnipeds; seabirds; elamobranchs; osteichthyes	Jereb and Roper (2010), Jereb et al. (2015)
Todaropsis eblanae	Fish; pelagic crustaceans; pteropods; other squid species, incl. cannibalism	Odontocetes; pinnipeds; seabirds; elamobranchs; osteichthyes	Jereb and Roper (2010), Jereb et al. (2015)
Ommastrephes bartramii	Fish; pelagic crustaceans; pteropods; other squid species, incl. cannibalism	Odontocetes; pinnipeds; seabirds; elamobranchs; osteichthyes	Watanabe et al. (2004), Jereb and Roper (2010)
Chiroteuthis calyx	n/a	Sperm whale and dolphins; pinnipeds; seabirds; blue shark; osteichthyes	Akimushkin (1965), Kubodera et al. (2007), Jereb and Roper (2010)
Mastigoteuthis agassizii	Crustaceans	n/a	Verrill (1881)
Teuthowenia megalops	n/a	Sperm whale, northern bottlenose whale, Cuvier´s beaked whale; blue shark; swordfish	Clarke (1966, 2006), Nixon (1983), Jereb and Roper (2010)
Galiteuthis armata	n/a	Sperm whale	Clarke (2006)
Galiteuthis phyllura	n/a	Sperm whale	Akimushkin (1965)

Table 2 (continued)

Species	Main prey	Main predators	References
Taonius borealis	n/a	Sperm whale; albatrosses; blue shark	Akimushkin (1965), Kubodera et al. (2007), Jereb and Roper (2010)
Rossia moelleri	Crustaceans; fish; echinoderms; actinians	Bearded seal, Walrus; cod, haddock	Grimpe (1933), Kondakov (1937), Muus (1962), Mercer (1968), Mehl (1991)
Rossia palpebrosa	Crustaceans; fish	Bearded seal; cod	Kondakov (1937), Mercer (1968), Mehl (1991)
Rossia macrosoma	Crustaceans	n/a	Boletzky and Boletzky (1973)
Rossia megaptera	Crustaceans; fish	n/a	Mercer (1968)
Rossia pacifica	Crustaceans; fish	n/a	Mercer (1968), Summers and Colvin (1989)
Sepietta oweniana	Fish; crustaceans: mysids, shrimps, euphausiids, amphipods; bivalves; polychaetes	Odontocetes; bottom fish; *Sepia officinalis* and *Eledone moschata*	Bergstrøm and Summers (1983), Bergstrøm (1985), Orsi-Relini and Massi (1988), Blanco et al. (1995), Santos et al. (1995), Golikov et al. (2014), Jereb et al. (2015)
Sepiola atlantica	Fish, crustaceans: mysids, shrimps	Odontocetes; bottom fish	Yau and Boyle (1996), Jereb et al. (2015)

n/a not available

[a]Diet and predators described in part of the cited literature are based on mixed samples from *Bathypolypus arcticus* and *B. bairdii*

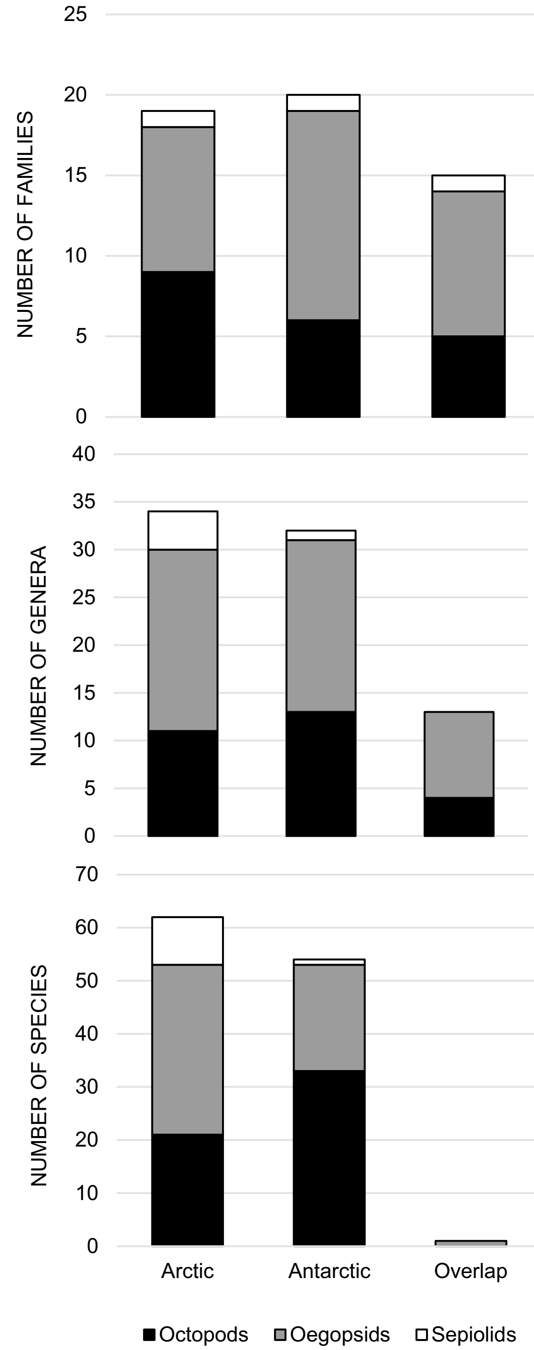

Fig. 3 Comparison of cephalopod diversity (at the family, genus and species levels) in the Arctic (including the Pacific Subarctic) and Antarctic regions

32 in the Arctic itself, the rest in the Pacific Subarctic, with almost no species inhabiting both areas), the Antarctic region has 54 species. The only species occurring at both poles is the giant squid *Architeuthis dux*, which is a foraging migrant from warmer temperate waters. Of all other known cephalopod species occurring in the Arctic and Antarctic, *Brachioteuthis riisei* (family Brachioteuthidae) is the

Table 3 Distribution of Antarctic cephalopods, either in Antarctic waters but extending further north, into sub_antarctic or warmer waters

Species	Bathymetry	Geographic range (within the studied area)	References
Opisthoteuthis hardyi (Opisthoteuthidae)	Slb	Atlantic (AW; SG) and SA	Villanueva et al. (2002), Collins et al. (2010)
Cirroctopus glacialis (Cirroctopodidae)	Sl	Atlantic (AW; SS, AP)	Robson (1930), Vecchione et al. (1998), Allcock (2014)
Cirroctopus mawsoni (Cirroctopodidae)	Sl	Indian (AW), Pacific (AW)	O'Shea (1999), Allcock (2014)
Cirrothauma magna (Cirroteuthidae)	B	Indian (AW/SA; PE/CR)	Guerra et al. (1998), Allcock (2014)
Cirrothauma murrayi (Cirroteuthidae)	B	Atlantic (A; SC)	Roper and Brundage (1972), Collins and Rodhouse (2006)
Stauroteuthis gilchristi (Stauroteuthidae)	Slb	Atlantic (AW; SG), Indian (SA; CR, KE)	Collins and Henriques (2000), Cherel et al. (2004), Collins et al. (2004)
Graneledone antarctica (Megaleledonidae)	B	Atlantic (AW; AP), Pacific (AW; RS), Indian?	Voss (1976), Vecchione et al. (2005), Allcock (2014)
Graneledone gonzalezi (Megaleledonidae)	Sl	Indian (AW/SA; KE)	Guerra et al. (2000)
Bathypurpurata profunda (Megaleledonidae)	Sl	Atlantic (AW; SS)	Vecchione et al. (2005)
Pareledone felix (Megaleledonidae)	Sl	Atlantic (AW; AP)	Allcock et al. (2007, 2011), Allcock (2014)
Pareledone turqueti (Megaleledonidae)	Sh, Sl	All (AW)	Kuehl (1988), Allcock (2005, 2014), Strugnell et al. (2012)
Pareledone charcoti (Megaleledonidae)	Sh, Sl	Atlantic (AW; SS, AP, SO)	Allcock (2005)
Pareledone aurorae (Megaleledonidae)	Sh, Sl	Indian (AW; Queen Mary Land, PB)	Lu and Stranks (1994), Allcock (2005, 2014)
Pareledone framensis (Megaleledonidae)	Sl	Indian (AW; Fram Bank)	Lu and Stranks (1994)
Pareledone aequipapillae (Megaleledonidae)	Sl	Atlantic (AW; SS), Pacific (AW)	Allcock (2005, 2014), Allcock et al. (2011)
Pareledone albimaculata (Megaleledonidae)	Sl	Atlantic (AW; SS)	Allcock (2005), Allcock et al. (2011)
Pareledone aurata (Megaleledonidae)	Sh, Sl	Atlantic (AW; SS)	Allcock (2005), Allcock et al. (2011)
Pareledone cornuta (Megaleledonidae)	Sh, Sl	Atlantic (AW; SS), Indian (AW, PB, Adélie land)	Allcock (2005, 2014), Allcock et al. (2011)
Pareledone panchroma (Megaleledonidae)	Sl	Atlantic (AW; SS), Pacific (AW, RS, Adélie land)	Allcock (2005, 2014), Allcock et al. (2011)
Pareledone serperastrata (Megaleledonidae)	Sh, Sl	Atlantic (AW; SS)	Allcock (2005)
Pareledone subtilis (Megaleledonidae)	Sh, Sl	Atlantic (AW; SS)	Allcock (2005, 2014), Allcock et al. (2011)
Pareledone prydzensis (Megaleledonidae)	Sl	Indian (AW; PB)	Lu and Stranks (1994), Allcock (2014)
Adelieledone polymorpha (Megaleledonidae)	Sh, Sl	Atlantic (AW)	Kuehl (1988), Allcock et al. (2001, 2003b), Collins et al. (2004), Allcock (2014)
Adelieledone adelieana (Megaleledonidae)	Sh, Sl	Indian (AW), Pacific (AW)	Lu and Stranks (1994), Allcock et al. (2003b), Allcock (2014)
Adelieledone piatkowski (Megaleledonidae)	Slb	Atlantic (AW; AP)	Allcock et al. (2003b), Allcock (2014)
Thaumeledone gunteri (Megaleledonidae)	Sl	Atlantic (AW; SG)	Yau et al. (2002), Allcock et al. (2004), Collins et al. (2004)
Thaumeledone rotunda (Megaleledonidae)	B	All (AW)	Allcock et al. (2004)
Thaumeledone peninsulae (Megaleledonidae)	Sl, B	Atlantic (AW; AP)	Allcock et al. (2004)
Praealtus paralbida (Megaleledonidae)	B	Atlantic (AW; AP)	Allcock et al. (2004)
Megaleledone setebos (Megaleledonidae)	Sh, Sl	All (AW)	Lu and Stranks (1994), Allcock et al. (2003c), Allcock (2014)

Table 3 (continued)

Species	Bathymetry	Geographic range (within the studied area)	References
Muusoctopus levis (Enteroctopodidae)	Sh	Indian (AW; HE)	Piatkowski et al. (1998), Allcock et al. (2001), Strugnell et al. (2011), Allcock (2014)
Muusoctopus thielei (Enteroctopodidae)	Sh	Indian (AW/SA; KE)	Bustamante et al. (1998), Strugnell et al. (2011), Allcock (2014)
Muusoctopus rigbyae (Enteroctopodidae)	Sl	Atlantic (AW; AP, SS)	Vecchione et al. (2009), Allcock (2014)
Architeuthis dux (Architeuthidae)	Mb	All (AW) and warmer waters	Vovk et al. (1975), Cherel (2003), Winkelmann et al. (2013)
Kondakovia longimana (Onychoteuthidae)	E, Mb	All (AW), also in SA	Cherel and Weimerskirch (1999), Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Onykia ingens (Onychoteuthidae)	Sh, B	All (SA) and warmer waters	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Filippovia knipovitchi (Onychoteuthidae)	Mb	All (AW)	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Onykia robsoni (Onychoteuthidae)	M	Warmer waters, occasionally in SA and rare in AW	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Gonatus antarcticus (Onychoteuthidae)	Mb	All (AW and SA) and possibly in warmer waters	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Histioteuthis atlantica (Histioteuthidae)	E, Mb	Warmer waters, common in A/SA boundary (KE)	Xavier et al. (1999, 2016b), Cherel et al. (2004), Rodhouse et al. (2014a) and references within
Histioteuthis eltaninae (Histioteuthidae)	Mb	All (SA), occasionally in AW and warmer waters	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Batoteuthis skolops (Batoteuthidae)	Mb	All (AW), occasionally in SA and rare in warmer waters	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Psychroteuthis glacialis (Psychroteuthidae)	Mb	All (AW), rare in SA	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Alluroteuthis antarcticus (Neoteuthidae)	M	All (AW), also occur in SA (KE, CR)	Xavier et al. (1999, 2016b), Cherel et al. (2004), Rodhouse et al. (2014a) and references within
Bathyteuthis abyssicola (Bathyteuthidae)	E, M	All (AW, SA and warmer waters)	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Slosarczykovia circumantarctica (Brachioteuthidae)	E, Mb	All (AW), occasionally in SA	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Martialia hyadesi (Ommastrephidae)	Sh, M	All (SA), occasionally in AW and warmer waters	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Chiroteuthis veranyi (Chiroteuthidae)	Mb	All (SA), occasionally in AW and warmer waters	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Asperoteuthis lui (Chiroteuthidae)	Mb	Warmer waters and SA, rare in AW (Atlantic; SG)	Arkhipkin and Laptikhovsky (2008), Braid (2017)
Mastigoteuthis psychrophila (Mastigoteuthidae)	Mb	All (AW)	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Galiteuthis glacialis (Cranchiidae)	E, Mb	All (AW), occasionally in SA and rare in warmer waters	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
Taonius sp. B (*Voss*) (Cranchiidae)	?	Warmer waters, common in SA and rare in AW	Xavier et al. (1999) and references within
Mesonychoteuthis hamiltoni (Cranchiidae)	B	All (AW) and SA (CR)	Xavier et al. (1999, 2016b), Rodhouse et al. (2014a) and references within
cf Stoloteuthis leucoptera (Sepiolidae)	Mb	Indian (KE)	Nesis (1987a), Cherel et al. (2004)

AW Antarctic waters, *SG* South Georgia region, *SS* South Shetland Islands region, *AP* Antarctic Peninsula region, *PE* Prince Edward Islands region, *PB* Prydz Bay, *CR* Crozet Islands region, *HE* Heard Island region, *KE* Kergulelen Island region, *SC* Scotia Sea, *RS* Ross Sea, *DR* Drake's passage, *SA* Sub-Antarctic waters, *SO* South Orkneys region, *WA* Western Antarctica, *B* bathyal, *E* epipelagic, *M* mesopelagic, *Mb* meso-bathypelagic, *Sl* slope, *Slb* slope-bathyal, *Sh* shelf, *Sl* slope)

Table 4 Diet and predators of Antarctic cephalopods

Species	Main prey	Main predators	References
Stauroteuthis gilchristi	n/a	Occur in Patagonian toothfish	Cherel et al. (2004)
Graneledone gonzalezi	n/a	Occur in Patagonian toothfish	Cherel et al. (2004)
Pareledone turqueti	Amphipods, egg masses, octopods, fish, polychaetes	Occur in Patagonian toothfish, Southern elephant seals and Antarctic fur seals	Lipinski and Woyciechowski (1981), Daneri et al. (2000), Xavier et al. (2002), Xavier and Cherel (2009) and references within
Pareledone charcoti	amphipods	Occur in Southern elephant seals	Daneri et al. (2000)
Adelieledone polymorpha	Amphipods, polychaetes	Occur in Southern elephant seals	Daneri et al. (2000), Xavier et al. (2002)
Megaleledone setebos	Ophiurids, amphipods, fish	n/a	Piatkowski et al. (2003)
Muusoctopus thielei	n/a	Occur in Patagonian toothfish and black-browed albatrosses	Cherel et al. (2000, 2002, 2004)
Muuscotopus rigbyae	Amphipods, crustaceans, ophiurids, fish		Piatkowski et al. (2003)
Architeuthis dux	n/a	Occur in wandering albatrosses, sleeper sharks and sperm whales	Clarke (1980), Cherel (2003), Xavier et al. (2003, 2014), Cherel and Duhamel (2004)
Kondakovia longimana	Fish, crustaceans (macroplankton: euphausiids, amphipods) and cephalopods (squid)	Albatrosses, penguins, bottlenose and sperm whales and sleeper sharks	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within
Onykia ingens	Fish (myctophids, bathylagids, other fish), crustaceans(euphausiids) and cephalopods	King penguins, wandering and royal albatrosses, pilot whales and the southern opah	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within
Filippovia knipovitchi	Fish (myctophids) and crustaceans (euphausiids: most Antarctic krill)	Sperm whales, grey-headed, black-browed and wandering albatrosses	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within
Onykia robsoni	Crustaceans	Not common in predators	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Gonatus antarcticus	Fish and crustaceans (euphausiids incl. Antarctic krill)	Patagonian toothfish, rockhopper and king penguins, wandering albatrosses and southern right-whale dolphins	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within
Histioteuthis atlantica	n/a	Porbeagle sharks and wandering albatrosses	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Histioteuthis eltaninae	n/a	Wandering, grey-headed, sooty and light-mantled sooty albatrosses	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Batoteuthis skolops	n/a	Patagonian toothfish, black-browed, grey-headed and yellow-nosed albatrosses	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Psychroteuthis glacialis	Fish (*Pleurogramma*, other fish) and crustaceans (euphausiids (incl. Antarctic krill))	Emperor penguins, sperm whales and elephant seals	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within
Alluroteuthis antarcticus	Fish (*Pleurogramma*, other fish), crustaceans (macroplankton: euphausiids (incl. Antarctic krill), amphipods) and cephalopods (squid)	Wide range of predators but never in high numbers	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within

Table 4 (continued)

Species	Main prey	Main predators	References
Bathyteuthis abyssicola	n/a	Very rare in predators	Collins and Rodhouse (2006), Xavier and Cherel (2009), Stevens et al. (2014) and references within
Slosarczykovia circumantarctica	Crustaceans (incl. Antarctic krill)	Wide range of predators but never in high numbers (except in Antarctic fur seals)	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Martialia hyadesi	Fish (myctophids), crustaceans(euphausiids, amphipods) and cephalopods	Grey-headed, black-browed and yellow nosed albatrosses, white-chinned petrels	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within
Chiroteuthis veranyi	n/a	Wide range of predators but never in high numbers	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Asperoteuthis lui	n/a	Wide range of predators but never in high numbers	Clarke (1980), Xavier et al. (2003, 2014)
Mastigoteuthis psychrophila	n/a	Wide range of predators but never in high numbers (except in Patagonian toothfish)	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Galiteuthis glacialis	Fish and crustaceans (macroplankton: euphausiids (incl. Antarctic krill), amphipods, copepods)	Black-browed, grey-headed and light-mantled sooty albatrosses	Collins and Rodhouse (2006), Xavier and Cherel (2009), Ratcliffe and Trathan (2011) and references within
Taonius sp. B (Voss)	n/a	Wandering albatrosses	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
Mesonychoteuthis hamiltoni	n/a	Sperm whales	Collins and Rodhouse (2006), Xavier and Cherel (2009) and references within
cf Stoloteuthis leucoptera	n/a	Occur in Patagonian toothfish and skates	Cherel et al. (2004)

only known species that is considered to be distributed so broadly that it may reach both the Arctic and the Southern Ocean (Jereb and Roper 2010). This species may comprise a species complex and taxonomic work is urgently needed to clarify its distributional range (Allcock and Barratt 2014). Indeed, two species from this family are known to occur close to or within Antarctic waters, *B. linkovskyi* (distributed in more northerly warmer waters, north of the APF) and *Slosarczykovia circumantarctica* (distributed in more Antarctic waters, mostly south of the APF) (Lipinski 2001; Cherel et al. 2004), with Antarctic records of *B. riisei* likely to be attributed to the latter squid species (Lea et al. 2002; Cherel et al. 2004), but work in progress is addressing this taxonomic issue (Marek Lipinski, pers. comm.).

Trophic ecology (predator and prey interactions)

Arctic

The diet of Arctic cephalopods includes mainly crustaceans and fish (Table 2), yet the data available are limited (except for *G. fabricii* and *Bathypolypus* spp.) and more studies are needed. While incirrate octopods and sepiolids generally tend to prey on benthic organisms (mostly crustaceans), the main prey of squid are fish and pelagic crustaceans. Cannibalism is also common, especially in squid (see Table 2). Unlike in the Antarctic, where the marine food web depends strongly on Antarctic krill *Euphausia superba*, there is no "main food prey" for bottom or pelagic cephalopods in the Arctic (Tables 2, 4).

As in other parts of the World's oceans, cephalopods in the Arctic (including the Pacific Subarctic) are important prey for fish, seabirds and cetaceans (Table 2). However, in the Arctic, cephalopods are not as important as in other parts of the World's oceans, due to their lower abundance (Golikov et al. 2017). Predator data are mostly only available from the Pacific Subarctic, or from predator species that do not live in the Arctic on a permanent basis. The most noticeable predators of the native Arctic species are the cetaceans, pinnipeds, Greenland shark *Somniosus microcephalus*, Atlantic cod *Gadus morhua*, Greenland halibut *Reinhardtius hippoglossoides* and also the squid *Gonatus fabricii*. Marine birds are believed to feed less on cephalopods than in the Antarctic, whereas a wide range of Arctic marine mammals seem to feed more on cephalopods (Table 2; see below).

Antarctic

Knowledge on the diet of cephalopods in Antarctic waters remains limited (Collins and Rodhouse 2006). Antarctic squid feed mostly on fish (e.g., *Pleuragramma antarcticum* over the shelf and myctophid fish in oceanic waters), crustaceans (particularly Antarctic krill and other euphausiids, along with amphipods) and squid (i.e., cannibalism) (Table 4). Their preferred prey generally shifts as they grow, with early life stages (juveniles) feeding mostly on crustaceans and switching to fish/bigger prey later in life (Rodhouse and Nigmatullin 1996; Rodhouse 2013) (Table 4). There is little information on the preferred prey of Antarctic octopuses, particularly due to their fast digestion, as approximately 14% of all octopod stomach contents are unidentifiable (Piatkowski et al. 2003). Nevertheless, it is clear that the relatively shallow water species *Pareledone charcoti* feeds predominantly on amphipods, while *Megaleledone setebos*, with its substantially more robust beak (Allcock et al. 2003c), apparently feeds on ophiuroids (Piatkowski et al. 2003). Observations on stomach contents of other octopod species (Table 4), as part of the same study, were based on a limited number of individuals, so more research is needed.

Antarctic cephalopods are prey for numerous predators, ranging from fish to air-breathing predators, such as seals, albatrosses, penguins and whales (Table 4). Despite the relatively numerous Antarctic octopod species, their consumption by predators is poorly documented. This could be attributed to the lack of studies of benthopelagic cephalopod predators (most studies are focused on commercial fish species) (Pilling et al. 2001; Stevens et al. 2014), and due to their beaks being very similar between octopod species (Xavier and Cherel 2009; Allcock 2014). In terms of Antarctic squid, numerous species occur in the diet of top predators, particularly *Kondakovia longimana*, *Onykia ingens, Filippovia knipovitchi, Gonatus antarcticus, Histioteuthis* spp., *Martialia hyadesi*, *Galiteuthis glacialis* and *Taonius* sp. B (Voss) with *Psychroteuthis glacialis* more abundant in predators feeding closer to the continent (Table 4).

Climate change

Arctic

Ocean warming per se is known to have a major impact on the ecology of Arctic cephalopods. In fact, the boreo-subtropical Atlantic squid species *Todaropsis eblanae*, *Teuthowenia megalops* and *Galiteuthis armata* are currently found up to more than 2000 km to the north of their previous northern range border (Sabirov et al. 2009, 2012; Golikov et al. 2013b). The common bobtail squid *Sepietta oweniana* has been found, for the first time in the Barents Sea, about 100 km to the north-east of the previously known range border (Golikov et al. 2014). Previous unusually high latitude records of boreal sepiolids are also connected to warm periods in the Atlantic (e.g., *Sepiola atlantica*, *S. pfefferi*, *Rossia macrosoma*) or they were located near the shelf part of the Bering Sea (*R. pacifica*) (Grimpe 1925, 1933; Grieg 1933b; Adam 1939; Bruun 1945; Muus 1959, 1962; Akimushkin 1965; Jonsson and Dagsson 1970). Another example of poleward migration linked to climate change is found in the squid *Gonatus fabricii*, which currently thrives in the eastern part of the Barents Sea and the western part of the Kara Sea—two areas previously thought to be too cold for this species (Golikov et al. 2012, 2013b). Thus, one may argue that most cases of unusual warm-water species of cephalopods in the Arctic (and possibly also in the Bering Sea but no data on cephalopod range shifts are available for this region) can be categorised as: (1) foraging migrations happening relatively regularly (e.g., *Todarodes sagittatus*, *Illex illecebrosus*, *Ommastrephes bartrami*, *Architeuthis dux* and *Japetella diaphana*) and (2) range expansions due to ongoing Arctic warming (e.g., *Todaropsis eblanae*, *Teuthowenia megalops*, *Sepietta oweniana*) (Golikov et al. 2014).

Some cephalopod species that live in the northern part of the North Sea and southern Norway do not cross the Faroe-Shetland Channel and Faroe-Iceland Ridge and thus do not enter the Arctic, namely *Eledone moschata*, *Loligo forbesii*, *L. vulgaris*, *Alloteuthis subulata* and *Sepiola aurantiaca* (Nordgaard 1923; Spaarck 1923; Grimpe 1925, 1933; Nielsen 1930; Grieg 1933b; Adam 1939; Muus 1959, 1962, Nesis 1985, 1987b, 2001, 2003). Also, dead shells of *Sepia* spp. are often found in the area (Spaarck 1923; Nielsen 1930), while cuttlefishes themselves do not reach the borders of subarctic areas (Xavier et al. 2016a). More research is needed to assess how recent climate change may affect the ranges of cephalopods related to the Arctic region in the future.

Ocean acidification is well-known in the Arctic, as in the other parts of the World's oceans (Feely et al. 2004; Orr et al. 2005; Hoegh-Guldberg et al. 2014). The pteropod *Limacina helicina*, which is among the most important pelagic species in the Arctic, is very vulnerable to ocean acidification due to its aragonitic shell, and its population has declined (Comeau et al. 2009). The effect of ocean acidification influence on the Arctic cephalopods has not yet been investigated, but will most probably be similar to that seen on temperate cephalopods.

Overall, the impact of climate change on the abundance of Arctic cephalopods is difficult to estimate, because quantitative data on their quantitative distribution are scarce and has only started to become available in the last few years. For example, both abundance and biomass of *G. fabricii* in the Barents Sea showed no correlation with climatic conditions in 2009–2012, while the abundance (but not biomass) of *R. palpebrosa* in the Barents Sea was correlated with climatic conditions [i.e., an integrated climate index involving water and air temperature and ice cover (Boitsov et al. 2012; Golikov et al. 2017)].

Antarctic

Despite knowledge gaps on the physiology, biology and ecology of Antarctic cephalopods, it is possible to provide a tentative assessment of how Antarctic cephalopods might respond to future climate change. The increase of temperature per se is unlikely to have a major effect on Antarctic cephalopods whose distribution extends from the Antarctic to sub-Antarctic regions. Yet, ocean warming may reduce the northern limit of species distributions, particularly where oceanic fronts shifting further south (Böning et al. 2008), with cascading impacts on marine biological productivity (Montes-Hugo et al. 2009). Indeed, the abundance of Antarctic krill might change in the future (Atkinson et al. 2004), and Antarctic cephalopods will probably be negatively affected unless Antarctic krill (and other cephalopod prey) are replaced by other highly abundant swarming crustaceans (e.g., other krill species, copepods, amphipods such as *Themisto gaudichaudii*) (Atkinson et al. 2012).

Although changes in sea ice extent may cause changes in the distribution of some species (Constable et al. 2014; Gutt et al. 2015), there are no cephalopod species known to be sea ice dependent to the extent of Antarctic krill (Xavier et al. 2015, 2016b; Xavier and Peck 2015). Changes in large-scale ocean circulation are unlikely to affect Antarctic squid, but changes in mesoscale oceanography may have a significant impact (Rodhouse 2013). Therefore, changes in ocean ecology driven by retreating sea ice may have a greater effect on cephalopod populations than the direct effect of ice retreat (Rodhouse 2013; Xavier et al. 2015).

The relative undersaturation of calcium carbonate ($CaCO_3$) in the Southern Ocean suggests that ocean acidification will have its greatest impacts in this part of the world's ocean if CO_2 emissions continue on their projected trajectory (Feely et al. 2004; Orr et al. 2005; Hoegh-Guldberg et al. 2014). Although the effects of ocean acidification on key biological processes of Antarctic cephalopods have not been investigated so far, based on the knowledge gathered with the temperate counterparts (squids and cuttlefishes), one can argue that ocean acidification may reduce metabolism, scope for growth and activity (Rosa and Seibel 2008; Rosa et al. 2013, 2014), enhance malformations of early life stages (Rosa et al. 2014), affect paralarval swimming performance (Zakroff et al. 2017), and elicit statolith structural changes (e.g., abnormal shape with increased porosity) (Kaplan et al. 2013; Navarro et al. 2016) in polar cephalopod fauna. Effects of ocean acidification on other molluscs and crustaceans, such as pteropods and Antarctic krill, have been investigated and it has been shown that their shells and their hatching success, respectively, can be affected (Bednaršek et al. 2012; Kawaguchi et al. 2013; Manno et al. 2016).

Final considerations

This review aims to provide a comparative, updated review of knowledge of cephalopod biodiversity in the polar areas. Information about polar cephalopod biodiversity is still limited in comparison to tropical or temperate waters (Tables 1, 2, 3, 4) (Boyle and Rodhouse 2005; Jereb and Roper 2005, 2010; Collins and Rodhouse 2006; Golikov et al. 2013b; Jereb et al. 2014; Rodhouse et al. 2014a), mostly because these regions hold no cephalopod fisheries and certain areas are still poorly sampled (Xavier et al. 2006, 2016b; Griffiths 2010). Indeed, larger size (and mature) cephalopods are still hard to catch using scientific nets, particularly in the Antarctic (Collins and Rodhouse 2006).

Are the cephalopod polar faunas similar to one another? At the species level, only one species occurs in both polar regions (see above). However, 13 genera and 15 families occur in both polar regions (Fig. 3, Tables 1, 3). From an evolutionary perspective, the major radiation that led to the lineages we recognise mostly as orders today, took place in the Jurassic and Cretaceous (Strugnell et al. 2009; Tanner et al. 2017). However, the formation of the Arctic, compared with the Southern Ocean, took place much more recently, and the cephalopod fauna of these regions reflects that. Ancient relic forms (Nautilida, Vampyromorpha, Spirulida) are absent from both polar oceans. The cephalopod fauna of the Arctic includes a minority of species (10) that constantly live in the high Arctic, with more species (32 including the high Arctic) that inhabit the marginal parts of the Arctic. The fauna of the Arctic today consists of Rossiinae, Bathypolypodidae, Cirrata and Gonatidae—groups of cephalopods which also inhabit deep-water areas in tropical and temperate latitudes (Jereb and Roper 2010; Jereb et al. 2014). This reflects the relatively young age of the modern Arctic basin, the shelf of which became ice-free after the Pleistocene ($<$ 11,700 years ago), leading to colonization of the shelf by deep-water psychrophilic groups (Nesis 1985, 1987b, 2001, 2003). Thus, the Arctic has a relatively young fauna with low endemism (Dayton et al. 1994). The only endemic species of the Arctic are *Muusoctopus sibiricus* and *Rossia moelleri*. No species are currently known as circumpolar in the Arctic (Nesis 1987b, 2001). The only pelagic species is *Gonatus fabricii*, which is epipelagic in the beginning of its life cycle, and meso-bathypelagic later (Kristensen 1983); none of the benthic species has pelagic larvae (Nesis 1987b).

The Antarctic was formed through the separation of the Antarctic continent from South America and Australia and the subsequent formation of the Antarctic Circumpolar Current (ACC). The opening of the Drake Passage and the Tasman gateway led to ACC development around 30 million years ago (Livermore et al. 2005; Scher et al. 2015), with more rapid cooling in the middle Miocene (ca 15 Ma). Consequently, the Antarctic has old fauna and a high level of endemism (Dayton et al. 1994). Indeed, the Antarctic is believed to be the centre of origin of some deep-water groups (including octopuses) (Gebruk 1994; Wilson 1998; Allcock 2005; Collins and Rodhouse 2006; Rogers 2007; Strugnell et al. 2008), evidence for which includes greater numbers of species with higher levels of endemism. Evidence from octopuses is that the lineage of Antarctic and deep-sea octopuses diverged around 33 million years ago (Ma), and radiated at 15 Ma, related to the development of the thermohaline circulation (Strugnell et al. 2008). Diversity of other groups (e.g., octocorals) has subsequently been shown to be similarly influenced by the development of the thermohaline circulation (Dueñas et al. 2016).

So, the cephalopod fauna of the Arctic has been in situ for a relatively short time and is similar to that found in deep water, whereas the cephalopod fauna of the Antarctic is more complex, comprising octopods that have evolved in situ over 30 million years, an endemic squid (e.g., *Psychroteuthis glacialis*) and a majority of squid species that can cross the APF but have also adapted to the cold temperatures over 30 million years.

From a trophic relations perspective, Arctic cod is an important link between top predators and lower trophic levels in the relatively long Arctic marine food web (Ainley and DeMaster 1990; Hobson and Welch 1992; Welch et al. 1992; Hop and Gjøsæter 2013; Murphy et al. 2016), which is long because of these additional fish levels between zooplankton and top predators. In the Antarctic, Antarctic krill plays an important role in the intermediate trophic levels, thus making the Antarctic marine food web south of the APF relatively short (although the Southern Ocean has recently been acknowledged as more complex than previously thought, including north of the APF) (Marr 1962; Rau et al. 1992; Everson 2000; Murphy et al. 2007, 2016; Cherel et al. 2011; Xavier and Peck 2015). Consequently, Arctic cephalopods (particularly oceanic squid) feed more on fish (and are generally at a higher trophic level) than Antarctic cephalopods that feed more on crustaceans (and are generally at a lower trophic level) (Tables 2, 4). Antarctica has more seabirds species (e.g., albatrosses, petrels, penguins) (Clements et al. 2017), and a wider range of Antarctic seabirds feed on cephalopods than do Arctic seabirds (Tables 2, 4). Similarly, a wider range of Arctic mammal species (e.g., whales, pinnipeds, porpoises, walrus) feed to a greater extent on cephalopods than do Antarctic mammals (Tables 2, 4), despite overall mammal species numbers not differing greatly between the poles (the Arctic has more species of seals and endemic taxa, such as walruses and polar bears, whereas the Antarctic has more species of baleen whales) (Laidre et al. 2004; Lowther 2018).

The Arctic fauna is possibly more affected by increasing temperature, with Arctic cephalopod species known to be increasing their ranges, and probably their abundance, as water temperature increases (Sabirov et al. 2009, 2012, Golikov et al. 2012, 2013b, 2014, 2016). The same is also known in other Arctic marine groups such as fish, bivalves, gastropods, crustaceans (Berge et al. 2005; Johannesen et al. 2012; Nekhaev 2013). There are no data on the influence of ocean acidification on Arctic cephalopods (due to the lack of such studies). There is also no information on range increase in Antarctic cephalopod species but, due to climate change, the range of Antarctic squids may be changes in mesoscale oceanography (indirect) changes of sea ice and increased of ocean acidification (Rodhouse 2013; Xavier et al. 2015, 2016b; Xavier and Peck 2015).

More studies are needed on basic biology and ecology of polar cephalopods including taxonomy (including genetics), age and growth, physiology, reproduction, diet and feeding ecology and population dynamics (Golikov et al. 2013b; Rodhouse 2013; Rodhouse et al. 2014b; Xavier et al. 2015). Furthermore, there is a need to understand how polar cephalopods may adapt and respond to environmental change.

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Compliance with ethical standards

Conflict of interest All authors declare no conflicts of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors (as it is a review paper).

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